# Six copepodid stages of Ridgewayia klausruetzleri, a new species of copepod crustacean (Ridgewayiidae: Calanoida) from the barrier reef in Belize, with comments on appendage development 

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#### Abstract

Ridgewayia klausruetzleri from the barrier reef in Belize differs from the five other Atlantic species of Ridgewayia in the morphology of the female genital complex and fifth leg of both females and males. Developmental patterns of setation suggest that there are six enditic lobes associated with the syncoxa and basis of maxilla 2 , and that the ramal segments are exopodal. The maxilliped has a distomedial lobe on its basis and five endopodal segments, three of which are added proximally from the penultimate segment during the copepodid phase of development. The first through fourth legs exhibit the common, and presumed ancestral, pattern of segmental development. Left and right endopods of the male fifth leg are one-segmented, a condition resulting from developmental convergence for the two rami. The male fifth leg also exhibits setal loss during development of the right endopod and both exopods.


Ridgewayia Thompson \& Scott, 1903 along with three other genera of epibenthic, pseudocyclopoidean calanoids, Brattstromia Fosshagen (in Fosshagen \& Iliffe 1991), Exumella Fosshagen 1970, and Placocalanus Fosshagen, 1970 comprise the copepod family Ridgwayiidae of Wilson (1958). Species of Ridgewayia are found around and in crevices and caves in coral reef habitats. Of the nine nominal species of Ridgewayia, five are found in the Atlantic Ocean, R. marki (Esterly, 1911a), R. gracilis Wilson, 1958, R. shoemakeri Wilson, 1958, R. wilsonae Fosshagen, 1970, and R. fosshageni Humes \& Smith, 1974. Ridgewayia typica Thompson \& Scott, 1903, R. canalis (Gurney, 1927), R. krishnaswamyi Ummerkutty, 1963, and R. flemingeri Othman \& Greenwood, 1988, are Indo-Pacific.

On 17 July 1989 specimens of a new species of Ridgewayia were collected from a solitary swarm of copepods off the northern cay of Tobacco Range in Belize. Tobacco

Range ( $16^{\circ} 54^{\prime} \mathrm{N}, 88^{\circ} 05^{\prime} \mathrm{W}$ ) is a group of four cays about 1 km from the lagoonal side of the barrier reef of Belize. The cays surround a shallow grass flat. The copepod swarm was collected in 3-6 m of water in an area of peat blocks which are fractured and slumped from the northwest shore of the northern cay (MacIntyre et al. 1989). No swarms were observed in June 1988, or subsequently in May 1992 and June 1993. The first description of the copepodid phase of development for a species of Ridgewayia is presented here from the six copepodid stages in the swarm.

## Methods

The copepods were fixed with $4 \%$ formaldehyde in $35 \%$ sea water and preserved in $0.5 \%$ propylene phenoxytol/4.5\% propylene glycol/95.0\% fresh water. In the laboratory, specimens were cleared in steps through $50.0 \%$ lactic acid $/ 50.0 \%$ fresh water to $100 \%$ lactic acid and stained by adding
a solution of chlorazol black E dissolved in $70.0 \%$ ethanol $/ 30.0 \%$ fresh water, or treated with a $15 \%$ solution of KOH in water and stained.

Prosome and urosome are designated Pr and Ur. First through sixth copepodid stages are designated CI to CVI; CVI is the adult. Thoracic and abdominal somites are numbered according to their appearance during development as interpreted from data of Hulsemann (1991). The first and oldest thoracic somite bears the maxilliped and is fused with the cephalon. The youngest is the seventh; among calanoids it is the only thoracic somite without an appendage. In adult calanoids the seventh is the first somite of the urosome, and in adult females it is fused to the second abdominal somite to form the genital complex. The first and oldest abdominal somite is the most posterior; it bears the caudal rami. The youngest is immediately anterior to the oldest, and the remaining abdominal somites increase in age, and decrease in numerical designation, anteriorly.

Cephalic appendages are abbreviated A1 $=$ antennule; $\mathrm{A} 2=$ antenna; $\mathrm{Mn}=$ mandible; $\mathrm{Mx} 1=$ maxillule; $\mathrm{Mx} 2=$ maxilla. Appendages on thoracic somites are $\mathrm{Mxp}=$ maxilliped (thoracopod 1); P1-5 = swimming legs (thoracopods 2-6). The caudal ramus is CR. Designations of appendage segments generally follow Huys \& Boxshall (1991) except for Mx2 and Mxp; exopod = Re ; endopod $=\mathrm{Ri}$; medial lobe of a segment $=\mathrm{li}$, lateral lobe $=$ le. Terminal segments of Mx2 are exopodal. Mxp has at most five endopodal segments.

Ramal segments on the thoracopods (Mxp and P1-5) are numbered by their appearance during development (Hulsemann 1991, Ferrari \& Ambler 1992, and here) and not proximal-to-distal as is the usual case for copepod descriptions. On the Mxp the distal segment is the first endopodal segment, and the second endopodal segment is immediately proximal to the first. The third endopodal segment is immediately distal to

Table 1.-Setation of the maxilliped of Ridgewayia klausruetzleri for stages CI-CVI; setation of syncoxa and basis (columns 1-6) is complete at CII while setation of endopodal segments $2-5$ is not complete until CVI. Lobes of the syncoxa (s1-s4), the basis (b) and its distomedial lobe (l), and the endopodal segments ( $n 1-n 5$ numbered by developmental age) are arranged from left, proximally, to right, distally. $a=$ segment not formed.

|  | s 1 | s 2 | s 3 | s 4 | b | 1 | $n 3$ | $n 4$ | $n 5$ | $n 2$ | $n 1$ |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| CI | 0 | 1 | 2 | 2 | 2 | 1 | $a$ | $a$ | $a$ | 1 | 4 |
| CII | 1 | 2 | 4 | 3 | 3 | 2 | 1 | $a$ | $a$ | 1 | 4 |
| CIII | 1 | 2 | 4 | 3 | 3 | 2 | 1 | 1 | $a$ | 2 | 4 |
| CIV | 1 | 2 | 4 | 3 | 3 | 2 | 2 | 2 | 1 | 2 | 4 |
| CV | 1 | 2 | 4 | 3 | 3 | 2 | 3 | 3 | 2 | 3 | 4 |
| CVI | 1 | 2 | 4 | 3 | 3 | 2 | 4 | 4 | 3 | 4 | 4 |

the basis. The fourth endopodal segment is immediately distal to the third. The fifth endopodal segment is the middle segment. On an Mxp with a 5 -segmented endopod, the second and first segments are more distal and the third and fourth segments are more proximal (Table 1 and Figs. 3E, 9G, 11 F ). On P1-5, the distal segment of a ramus is the first segment. The second segment is immediately distal to the basipod. If present, the third segment is immediately proximal to the distal (or first) segment. For a 3-segmented ramus, the proximal segment is the second segment, the middle segment is the third segment, and the distal segment is the first segment (Figs. 4F, 7B, 9J). The number of setae recorded for the segments follows this same scheme.

Armament elements of appendages here are termed setae regardless of their position or degree of rigidity. Examples of the position and morphology of setae are shown in the illustrations. Two setae and one aesthetasc on a segment of A1 are designated $2+1$. Setules are epicuticular extensions of a seta; denticles are epicuticular extensions of an appendage segment; spinules are epicuticular extensions of a somite. Von Vaupel Klein's organ (Ferrari \& Steinberg 1993) on P1 (the appendage of thoracic somite 2) consists of the curved basipodal seta,


Fig. 1. Ridgewayia klausruetzleri n. sp., CVI female: A, animal left lateral; B, genital complex, right lateral; C, genital complex, ventral; D, rostrum right lateral; E, rostrum ventral; F, CR dorsal. CVI male: G, Th 6-7 and abdominal somites. Line $1=0.1 \mathrm{~mm}$ for $A$; line $2=0.1 \mathrm{~mm}$ for $G$; line $3=0.1 \mathrm{~mm}$ for $B-F$.
and distolateral corner of the second endopodal segment. Many setae on P1-5 of Ridgewayia narrow abruptly distally; setules usually are present only on the distal section.

## Ridgewayia klausruetzleri, new species

 Figs. 1-11Material. - CI-528 specimens; CII-505 specimens; CIII-403 specimens; CIV-319
specimens; CV -636 specimens; CVI3687 specimens from Tobacco Range ( $16^{\circ} 54^{\prime} \mathrm{N}, 88^{\circ} 05^{\prime} \mathrm{W}$ ) in Belize are deposited in the National Museum of Natural History, Smithsonian Institution (USNM). An undissected female holotype (USNM 268277), an undissected male allotype (USNM 268278), and one lot of undissected paratypes, 10 females and 10 males (USNM 268279) are in vials of glycerin. The re-
maining specimens (CI-524, CII-497, CIII-394, CIV-279, CV-596, CVI3663) comprise a lot of undissected paratypes (USNM 268280) in $0.5 \%$ propylene phenoxytol/4.5\% propylene glycol/95.0\% fresh water.

CVI female. - Length range of 15 specimens $0.84-0.90 \mathrm{~mm}$ (mean 0.87 ); average Pr length/Ur length $=3.1$.

Pr (Fig. 1A): 6 segments; 1st a complex of 5 cephalic somites plus thoracic somite 1 ; thoracic somites $2-6$ are simple and articulated.

Ur (Fig. 1A): 4 segments; 1st a genital complex of thoracic somite 7 and abdominal somite 2 (Fig. 1B); genital complex slightly asymmetrical, as viewed ventrally (Fig. 1C); several sensilla near left posterolateral corner. Copulatory and oviducal openings separate. Abdominal somites 3, 4, 1 articulated; somite 1 small.

Rostrum (Fig. 1D, E): a short thick plate.
A1 (Fig. 2A-C): 26 articulated segments with $1+1,4+1,2,2+1,2+1,2+1$, $2+1,2+1,2+1,2+1,2+1,2+1$, $2+1,2+1,2+1,2+1,2+1,2,2,2$ $+1,1,1,2,2+1,2,4+2$ setae + aesthetascs; 13th through 22 nd segments with row of small denticles.

A2 (Fig. 4A): coxa with 1 seta; basis with 2 setae. Re 8 -segmented with $1,1,1,1,1$, 1, 1, 4 setae. Ri 2-segmented with 1, 15 (7 terminal, 8 subterminal) setae.

Mn (Fig. 4B, C): coxa more heavily sclerotized medially; basis with 4 setae. Re 4 -segmented with 1, 1, 1, 3 setae. Ri 1 -segmented with 15 setae ( 11 terminal, 4 subterminal).

Mx1 (Fig. 3A, B): le with 9 setae. Re 1 -segmented with 11 setae. Basis with 5 setae; Ri with sets of 4 and 4 medial, and 7 terminal setae. Li 2 and 3 with 5 and 4 setae. Li 1 with 9 apical, 1 anterior setae and 4 posterior setae; denticles on posterior surface.

Mx2 (Fig. 3C): li $1-4$ of coxa with 5,3 , 3,3 setae; li 5 and 6 of basis with 4 and 3 setae. Re indistinctly segmented with 7 setae.

Mxp (Fig. 3D, E): syncoxa with 4 lobes of $1,2,4,3$ setae; basis with 5 setae ( 2 on a distal medial lobe). Ri 5 -segmented with $4,4,4,4,3$ setae. Three areas of denticles on coxa and a longitudinal row of denticles on basis.

Pl (Fig. 5A, B): coxa with medial seta; basis with curved, medial seta. Re 3 -segmented with 7, 2, 2 setae. All segments with row of denticles toward distal edge; segment 2 with longer denticles at distolateral corner; distolateral margin of segment 3 with a finger-like process with denticles along outer margin and an attenuate process. Ri 3 -segmented with 6, 1, 2 setae. Von Vaupel Klein's organ includes setules and seta of basis, and denticles and 2 pores on an attenuate distolateral edge of segment 2.

P2 (Fig. 4D): coxa with medial seta and lateral area of denticles; basis with medial area of denticles. Re 3 -segmented with 8,2 , 2 setae; segments 1 and 3 with row of denticles toward distal edge. Ri 3-segmented with $8,1,2$ setae.

P3 (Fig. 4E): coxa with medial seta and lateral denticles; basis unarmed. Re 3-segmented with 9, 2, 2 setae; posterior face of segments 1 and 3 with denticles toward distal edge. Ri 3 -segmented with 8,1 , 2 setae; posterior face of segment 3 with denticles toward distal edge.

P4 (Fig. 4F): coxa with medial seta, and lateral and anterior denticles; basis with lateral seta. Re 3-segmented with 9, 2, 2 setae; posterior face of segments 1 and 3 with denticles toward distal edge. Ri 3-segmented with $7,1,2$ setae.

P5 (Fig. 5C): coxa unarmed; basis with lateral seta and posterior denticles. Re 3 -segmented with $8,1,2$ setae; segment 1 with denticles on anterior face. Ri 2-segmented with 7, 0 setae.

CR (Fig. 1F): 5 terminal setae of differing lengths, and a small dorsal seta.

CVI male. - Differs from CVI female as follows: length range of 15 specimens $0.77-$ 0.82 mm (mean 0.79); average Pr length/Ur length $=3.0$.


Fig. 2. Ridgewayia klausruetzleri n. sp., CVI female: A, A1 articulated segments 1-9; B, A1 articulated segments $10-20$; C, A1 articulated segments 21-26. CVI male: D, right A1 articulated segments $1-10$; E, right Al articulated segments $11-18 ;$ F, right Al articulated segments $19-21$. Line $=0.1 \mathrm{~mm}$.


Fig. 3. Ridgewayia klausruetzleri n. sp., CVI female: A, Mx1 anterior; B, lil of Mx1 posterior; C, Mx2 posterior; D , syncoxa and basis of Mxp posterior; E, endopod of Mxp posterior (numbers to the right indicate the appearance of endopodal segments during development). Line $=0.1 \mathrm{~mm}$.


Fig. 4. Ridgewayia klausruetzleri n. sp., CVI female: A, A2; B, coxa of Mn; C, palp of Mn; D, P2 posterior, exopod detached; E, P3 posterior, exopod detached; F, P4 posterior, exopod detached (numbers to the right indicate the appearance of exopodal segments during development). Line $=0.1 \mathrm{~mm}$.


Ur (Fig. 1G): 5 somites; thoracic somite 7 with left lateral genital aperture. Abdominal somites $2,3,4,1$ simple and articulated; somite 1 small.

Right A1 (Fig. 2D-F): 21 articulated segments with: $2+1,3+1,2,2+1,2+1$, $2+1,2+1,2+1,4+2,2+1,5+3$, $2+1,2+1,2+1,2,2,3+1,2,2+1$, $2,3+3$ setae + aesthetascs; segments $11-$ 16 with row of denticles and segment 17 with 3 rows. Partly complete arthrodial membrane in segment 9; 2 partly complete ventromedial arthrodial membranes in segment 11 ; segment 17 probably of 3 fused segments based on 3 rows of denticles. Geniculation between 17th and 18th articulated segments.

P5 (Fig. 5D-G): right coxa unarmed; basis with lateral seta, and long, medial sensilla proximally and short medial denticles distally. Re 2 -segmented with 2, 1 setae; 3 ridged pads distally on segment 1. Ri 1 -segmented with midlateral seta and denticles.

Left coxa unarmed; basis with lateral seta. Re 3-segmented with 4, 1, 1 setae. Re1 hooklike, articulating at medial corner with 3rd segment; its proximal seta with 3 bends and an extension of its hyaline membrane on convex surface of the 3rd bend; 2nd and 3rd seta simple; 4th seta with 1 bend and an extension of its hyaline membrane on concave surface of the bend. Re2 outer, spinelike seta reaching to distal edge of Re3. Re3 outer, spine-like seta not reaching beyond setae of Rel. Ri 1-segmented, unarmed.

CV female. - Differs from CVI female as follows: length range of 27 specimens $0.73-$ 0.80 mm (mean 0.76 ); average Pr length/Ur length $=3.0$.

Ur (Fig. 6A, B): 4 segments; thoracic somite 7 and abdominal somites $2,3,1$ articulated. Arthrodial membrane between Th7 and Ab2 not as pronounced as those between other somites. Copulatory opening apparently forms at articulation of Th7 and Ab2 (Fig. 6B).

A1 (Fig. 6C): articulating segments 4-14
with $2+1,2,2+1,2,2+1,2,2+1,2$, $2,2,2+1$ setae + aesthetascs.

A2 (Fig. 6D): Ri terminal segment with 14 setae ( 7 terminal, 7 subterminal).

Mx1 (Fig. 6E): Re with 10 setae. Ri with medial sets of 3 and 4 setae, and 6 terminal setae.

Mxp (Fig. 6G): Ri 5 -segmented with 4, 3, 3, 3, 2 setae.

P1: Re2 distal margin simple; Re3 (Fig. 6F) distal margin with 2 simple extensions of segment. Ri2 without denticles or pores and elongation of distolateral margin less pronounced.

P5 (Fig. 6H): coxa unarmed; basis with lateral seta. Re 2 -segmented with 9, 1, setae.
Ri 2-segmented with 6, 0 setae.
CV male. -Differs from CV female as follows: length range of 13 specimens 0.68 0.74 mm (mean 0.71 ); average Pr length/Ur length $=3.0$.

Ur (Fig. 6I): pronounced arthrodial membrane between Th7 and Ab2.

P5 (Fig. 6J): right Re 2 -segmented with 7, 1 setae. Ri 2 -segmented with 4, 0 setae.

Left Re 2 -segmented with 7, 1 setae. Ri an unarmed segment.

CIV female. - Differs from CV female as follows: length range of 27 specimens 0.64 0.69 mm (mean 0.66 ); average Pr length/Ur length $=3.1$.

Ur (Fig. 7A): 3 segments; thoracic somite 7 and abdominal somites 2,1 articulated.

A1 (Fig. 8A, B): 25 segments with $1+1$, $2+1,1,1+1,1,1+1,1,1,2+1,1,1$, $2+1,2,1+1,2,2+1,2,2,2+1,1,1$, $2,2+1,2,4+2$ setae + aesthetascs; denticle rows on 13 th through 21 st segments.

A2 (Fig. 8C): Ri terminal segment with 13 setae ( 7 terminal, 6 subterminal).

Mn (Fig. 8D): Ri with 3 and 8 setae on segments 1 and 2.

Mx1 (Fig. 8E): basis with 4 setae. Re with 8 setae. Ri with medial sets of 3 and 3 setae, and 5 terminal setae.

Mxp (Fig. 8F): Ri 5 -segmented with 4, 2, 2, 2, 1 setae.



Fig. 7. Ridgewayia klausruetzleri n. sp., CIV female: A, body right lateral; B, exopod and endopod of P2 (numbers to the right indicate the appearance of exopodal segments during development); C , exopod and endopod of P3; D, exopod and endopod of P4; E, basis, exopod and endopod of P5. CIV male: F, basis, left exopod and endopod, and right endopod of P5. Setae which were broken and not studied are designated with a wavy-line cutoff. Line $1=0.1 \mathrm{~mm}$ for A ; line $2=0.1 \mathrm{~mm}$ for $\mathrm{B}-\mathrm{F}$.

P1 (Fig. 8G): Re 2-segmented with 8, 2 setae. Ri 2-segmented with 8,1 setae.

P2 (Fig. 7B): Re 2-segmented with 9, 2 setae. Ri 2 -segmented with 8,1 setae.

P3 (Fig. 7C): Re 2-segmented with 9, 2 setae. Ri 2 -segmented with 8,1 setae.

P4 (Fig. 7D): Re 2-segmented with 9, 1 setae; segment 2 with medial denticles. Ri 2 -segmented with 7, 1 setae.

P5 (Fig. 7E): basis unarmed. Re 1 -segmented with 7 setae. Ri 1-segmented with 4 seta.


Fig. 8. Ridgewayia klausruetzleri n. sp., CIV female: A, A1 articulated segments 1-17; B, A1 articulated segments 18-25; C, endopod 2 of A2; D, endopod of Mn; E, basis, exopod and endopod of Mx1; F, distomedial lobe of basis and endopod of $\mathrm{Mxp} ; G$, exopod and endopod of Pl . Line $=0.1 \mathrm{~mm}$.

CIV male. - Differs from CIV female as follows: length range of 13 specimens 0.62 0.65 mm (mean 0.64); average Pr length/Ur length $=3.0$.

P5 (Fig. 7F): right basis unarmed. Re 1 -segmented with 7 setae. Ri 1 -segmented with 4 setae.

Left basis unarmed. Re 1-segmented with 7 setae. Ri 1-segmented without setae.
CIII. - Differs from CIV female as follows: length range of 25 specimens 0.50 0.58 mm (mean 0.54 ; average Pr length/UR length $=3.4$.

Ur (Fig. 9A): 2 segments; thoracic somite 7 and abdominal somite 1 articulated.

A1 (Fig. 9B, C): 24 articulated segments with $1,1+1,1,1+1,0,1,0,1+1,0$, $1,1,1,1+1,1,1,1,1,2+1,1,1,2,2$ $+1,2,4+2$ setae + aesthetascs.

A2 (Fig. 9D): Ri terminal segment with 11 setae ( 6 terminal, 5 subterminal).

Mn (Fig. 9E): Ri2 with 7 apical setae.
Mx1 (Fig. 9F): le with 8 setae. Ri 2-segmented; Ril with medial groups of 2 and 3 setae. Lil with 7 apical setae, 1 reduced in length.

Mxp (Fig. 9G): Ri 4-segmented with 4, 2, 1, 1 setae.

P1 (Fig. 9H): proximal 3 setae of Ril and seta of Ri2 reduced in size.

P2: proximal, medial seta of Re1 and medial seta of Re 2 reduced in size. Proximal, medial 2 setae of Ril and medial seta of Ri2 reduced in size.

P3 (Fig. 9I): Re 2 -segmented with 7, 1 setae. Ri 2-segmented with 7, 1 setae.

P4 (Fig. 9J): coxa and basis unarmed. Re 1 -segmented with 7 setae. Ri 1 -segmented with 6 setae.

P5 (Fig. 9K): ventrally-directed bud with 2 medial and 3 apical setae.
CII. - Differs from CIII as follows: length range of 25 specimens $0.44-0.47 \mathrm{~mm}$ (mean 0.46 ); average Pr length $/$ Ur length $=2.9$.
$\operatorname{Pr}$ (Fig. 10A): 5 segments; 1st a complex of 5 cephalic somites plus thoracic somite 1 ; thoracic somites $2-5$ simple and articulated.

Ur (Fig. 10A): 2 segments; thoracic somite 6 , with lateral lobes, and abdominal somite 1 articulated.

A1 (Fig. 10B, C): 17 articulated segments with $1,2+2,0,1,0,1+1,0,1,0,1,1$ $+1,1,1,1,2+1,2,4+2$ setae + aesthetascs; denticles on segments 12 and 13.

A2 (Fig. 10D): Ri terminal segment with 10 (6 terminal, 4 subterminal) setae.

Mx1 (Fig. 10E): le with 5 setae. Re 1 -segmented with 7 setae. Basis with 3 setae. Ril with medial sets of 2 and 2 setae. Lil with 2 posterior setae; li2 with 4 setae.

Mx2 (Fig. 10F): li 5 and 6 of basis with 3 and 1 setae. Re indistinctly segmented with 6 setae.

Mxp (Fig. 10G): Ri 3-segmented with 4, 1, 1 setae.

P1 (Fig. 10H): Re 2-segmented with 8, 1 setae. Ri 2-segmented with 7, 1 setae.

P2 (Fig. 10I): Re 2-segmented with 7, 1 setae. Ri 2-segmented with 7, 1 setae.

P3 (Fig. 10J): coxa unarmed. Re 1 -segmented with 7 setae. Ri 1 -segmented with 6 setae.

P4 (Fig. 10K): ventrally-directed bud with 2 medial, 1 lateral, and 2 apical setae.
CI. - Differs from CII as follows: length range of 25 specimens $0.36-0.40 \mathrm{~mm}$ (mean 0.38 ); average Pr length/Ur length $=2.6$.
$\operatorname{Pr}$ (Fig. 11A): 4 segments; articulation between thoracic somites 3 and 4 not as distinct as between other segments.

Ur (Fig. 11A): 2 segments; thoracic somite 5 , with lateral lobes, and abdominal somite 1 articulated.

Rostrum absent
A1 (Fig. 11B): 10 articulated segments with $3,1+1,1,1+1,0,1,1,2+1,2$, $4+2$ setae + aesthetascs; denticles absent.

A2 (Fig. 11C): Ri terminal segment with 8 (5 terminal, 3 subterminal) setae.

Mn (Fig. 11D): Ri2 with 5 setae.
Mx1 (Fig. 11E): le with 4 setae. Ri with medial groups of 2 and 1 setae. Li2 with 2 setae.

Mxp (Fig. 11F): syncoxa with 4 lobes of $0,1,2,2$ setae; basis with 3 ( 1 on a distal


Fig. 9. Ridgewayia klausruetzleri n. sp., CIII: A, body left lateral; B, A1 free segments 1-15; C, A1 free segments 16-24; D, endopod 2 of A2; E, endopod 2 of Mn ; F, Mx1; G, distomedial lobe of basis and endopod of $\operatorname{Mxp}$ (numbers to the right indicate the appearance of endopodal segments during development); $H$, endopod of P1; I, exopod and endopod of P3; J, exopod and endopod of P4 (number to the left indicates the appearance of exopodal segment during development); K, P5. Setae which were broken and not studied are designated with a wavy-line cutoff. Line $1=0.1 \mathrm{~mm}$ for A ; line $2=0.1 \mathrm{~mm}$ for $\mathrm{B}-\mathrm{K}$.


Fig. 10. Ridgewayia klausruetzleri n. sp., CII: A, body right lateral; B, A1 articulated segments 1-10; C, A1 articulated segments 11-17; D, endopod 2 of $A 2$; $E, M x 1 ; F$, distal lobes of basis and exopod of $M x 2$; G, basis and endopod of Mxp; H, exopod and endopod of P1; I, exopod and endopod of P2; J, P3; K, P4. Setae which were broken and not studied are designated with a wavy-line cutoff. Line $1=0.1 \mathrm{~mm}$ for A ; line $2=0.1 \mathrm{~mm}$ for $\mathrm{B}-\mathrm{K}$.


Fig. 11. Ridgewayia klausruetzleri n. sp., CI: A, animal right lateral; B, A1; C, endopod 2 of A2; D, endopod 2 of $\mathrm{Mn} ; \mathrm{E}, \mathrm{Mxl} ; \mathrm{F}, \mathrm{Mxp}$ (numbers to the right indicate the appearance of endopodal segments during development); G, P1; H, P2; I, P3. Setae which were broken and not studied are designated with a wavy-line cutoff. Line $1=0.1 \mathrm{~mm}$ for A ; line $2=0.1 \mathrm{~mm}$ for $\mathrm{B}-\mathrm{I}$.
medial lobe) setae. Ri 2-segmented with 4, 1 setae.

P1 (Fig. 11G): coxa and basis unarmed. Re 1 -segmented with 8 setae. Ri 1 -segmented with 7 setae.

P2 (Fig. 11H): coxa and basis unarmed. Re 1 -segmented with 7 setae. Ri 1 -segmented with 6 setae.

P3 (Fig. 11I): ventrally-directed bud with 2 medial and 3 apical setae.

Remarks. - The six Atlantic species of Ridgewayia can be divided into two groups. In the first group, of $R$. klausruetzleri, $R$. marki, R. shoemakeri, and R. fosshageni, the endopod of the male left P5 is a relatively simple, unarmed segment. In the second group, of $R$. wilsonae and $R$. gracilis, this segment is divided into several fingerlike extensions. Females of the second group can be separated from each other by the number of setae on the endopod of the female P5, six on $R$. wilsonae or seven on $R$. gracilis.

Among males in the first group, the external spine-like seta on the third (middle) exopodal segment of the left P5 of R. shoemakeri and $R$. fosshageni extends beyond the setal elements of the first (distal) segment; in R. klausruetzleri and R. marki, as redescribed by Yeatman (1969), this seta does not extend beyond the smallest of these elements. An examination of specimens of R. marki deposited in the National Museum of Natural History by Dr. Harry Yeatman (USNM 190873) shows that $R$. marki can be separated from R. klausruetzleri by the following characters. Ridgewayia klausruetzleri is smaller (length range of adult females $0.84-0.90 \mathrm{~mm}$, males $0.77-$ 0.82 mm ) than $R$. marki (females 0.98 1.05 mm , males $0.90-1.03 \mathrm{~mm}$ ). The copulatory pore is located more anteriorly on the female genital complex of $R$. klausruetzleri (compare Figs. 1B, C with 12A, B). The distomedial corner of the second (proximal) endopodal segment of the female P5 is not as pronounced as that of $R$. marki (compare Figs. 5C with 12C). The external, spine-like
seta of the third (middle) exopodal segment of $R$. klausruetzleri reaches slightly beyond the second seta of the first (distal) segment, while in $R$. marki this spine reaches to the edge of the distal spine-like seta of the first segment. The right basis of the male P5 of R. klausruetzleri has a set of long sensilla proximally and a set of short denticles distally; males of $R$. marki (compare Figs. 5F and 12D) have a pad-like thickening distally but no proximal sensilla. The right endopodal seta is located on the distal half of the outer margin in $R$. klausruetzleri but on the proximal half in $R$. marki. The external, spine-like seta on the second (proximal) segment of the left exopod of $R$. klausruetzleri reaches to the end of the well-developed outer tip of the third (middle) segment; in R. marki this spine reaches beyond the poorly developed tip (Fig. 12D).

Ecological notes. - No other calanoid copepods were collected in the swarm of copepodids of $R$. klausruetzleri; no nauplii were present. The copepods appeared colorless in the water, but after capture all stages appeared red in direct sunlight. Examination of live specimens with a dissecting microscope indicated that pigment was concentrated at margins of body somites. This color pattern is not apparent in preserved specimens today. Number (and percentage) of each copepodid stage of $R$. klausruetzleri in the swarm were as follows: CI-528 (8\%); CII-505 (8\%); CIII-403 (7\%); CIV-319 (5\%); CV-636 (11\%); CVI-3687 (61\%). This aggregation like other calanoid swarms (Kimoto et al. 1988) includes CI, and contrasts with swarms of the cyclopoid copepod Dioithona oculata (Farran, 1913) which seldom include this stage (Ambler et al. 1991). Percentage of females in the last three stages was CIV-68\%; CV-68\%; CVI-74\%; females and males of the CIV and CV cannot be determined without dissection so percentages for those stages were estimated from a subsample of 40 specimens.

Identities and homologies.-Ferrari \& Steinberg (1993) have noted for Scopalatum


Fig. 12. Ridgewayia marki (Esterly, 1911a), CVI female: A, genital complex ventral; B, genital complex lateral; C, P5 posterior, exopod detached. CVI male: D, P5 posterior; E, left exopod 1 and 3 of P5 anterior. Line $1=0.1 \mathrm{~mm}$.
vorax (Esterly, 1911b) that the setation of the distal part of maxilla 2 is complete by CII. This early completion of setation is similar to the setal development of the exopods of antenna 2 and mandible, but it is unlike any known endopodal pattern for anterior copepod appendages. Thus the distal part of maxilla 2 is considered an exopod. The setation of $R$. klausruetzleri develops similarly. The sixth lobe of maxilla 2 is considered a lobe of the basis and not an endopodal segment (Huys \& Boxshall 1991). It is not an endopodal segment because its setation is complete at CII; it is not an exopodal segment because, like the other enditic lobes, it bears more than 1 seta.

New endopodal segments of the maxilliped (segments 3-5) are formed within the penultimate segment (Figs. 10G \& 11F); the antepenultimate segments of CII, CIII, and CIV are the new ones. The distomedial lobe of the basis, which is antepenultimate at CI, adds its last seta at CII. This early completion of setation proceeds identically to that of the syncoxal lobes and non-ramal segments of other appendages, and suggests that this lobe is part of the basis (Von Vaupel Klein 1982) and not a sixth endopodal segment (Huys \& Boxshall 1991).

Each new endopodal segment of the maxilliped initially possesses a single seta (Table 1), but setae also are added to non-terminal segments (including the new segments) at CIV, CV, and CVI so that there are two kinds of setae on the new segments: one seta formed as the segment is formed and several setae added after the segment has formed. On the remaining thoracopods, the inner seta of the second (proximal) exopodal segment of thoracopods $2-5$ (swimming legs $1-4$ ) is the only seta added after segmentation.

Segmentation of P1-4 appears to follow the common pattern of development which is presumed to be ancestral for copepods (Ferrari 1988). P1 and P2 develop similarly. Although the morphology of the last naupliar stage is unknown, P1 and P2 are re-
organized appendages with 1 -segmented rami at CI ; these rami gain a second segment at CII, after which there is no further segmentation until CV. P3 develops serially and similarly, but one stage out of register with P1 and P2. It is a bud at CI, is reorganized at CII, and adds its second segment at CIII. P4 develops serially, but one stage out of register with P3; it is a bud at CII, is reorganized at CIII, and adds its second segment at CIV. P1-4 add their third ramal segments simultaneously during the molt to CV.

The number of outer setae on the third (middle) exopodal segment of P1 in species of Ridgewayia has been interpreted as one or three elements (Wilson 1958, Humes \& Smith 1974, Yeatman 1969). Most copepods have one external seta on the third (middle) exopodal segment. Ridgewayia klausruetzleri has one seta (an articulating element whose thick base narrows abruptly; this morphology is identical to that of the other setae on the swimming leg segments); the two structures medial to the seta do not articulate and instead are complex attenuations of the segment. This interpretation is clearer at CV because generally there is no change in the number of setae from CV to CVI. In CV R. klausruetzleri there is one abruptly narrowing seta and two simple attenuations of the segment (Fig. 6F); the latter two presumably will become the complex attenuations of CVI.

The left and right endopods of the male P5 are one-segmented, but they develop by different patterns. At CIV the left endopod is an unarmed segment; neither segments nor setae are added during later development. At CIV the right endopod is one-segmented with four setae. A second, unarmed segment is added proximally at CV and there is no change in setation. At CVI the endopod is again one-segmented and just one seta is present. The development of the other three setae and the arthrodial membrane between the two segments present at CV presumably is repressed.

Setae also are lost during the exopodal development of male P5. Both the left and right exopods are two-segmented with seven and one setae at CV. At CVI five setae are lost from the first (distal) segment of the right exopod. Two are lost from the first (distal) segment of the left exopod as one seta becomes associated with the new, third (middle) segment.

Etymology. - This species honors Dr. Klaus Ruetzler for his continued support of, and contributions to coral reef research.

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